Zonation of Marine Gastropods on a Rocky Intertidal Shore in the Admiralty Gulf, Western Australia, with Emphasis on the Genus *Nerita*

BY

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(3 Text figures)

INTRODUCTION

THE ZONATION OF MARINE MOLLUSCS along the intertidal shorelines of the world has been intensively investigated in many areas since the broad perspectives of the Stephensons were published (STEPHENSON & STEPHENSON, 1949). A number of more recent studies have investigated the zonation of marine molluscs on the eastern and southern coasts of Australia (ENDEAN *et al.*, 1956; UNDERWOOD, 1972) or have examined particular features of the biology of intertidal molluscs occurring on those shores (COLEMAN, 1976; UNDERWOOD, 1975, 1976). Development of our understanding of the marine intertidal communities of Western Australia has been severely handicapped by the size of the coastline, about 6500 km, and the small number of marine biologists in the state. The marine intertidal communities of the Perth area have been examined (HODGKIN, MARSH & SMITH, 1955; MARSH & HODGKIN, 1962; PRIDEAUX, 1976) but there is almost no published information available on any aspect of the molluscan communities of the north coast of Western Australia east of Derby. The coastline of that area has been largely inaccessible from land because of a lack of roads and access from the sea has been prevented by the lack of available ship-time. Over the last several years the Western Australian Museum has conducted several field programs in the northeastern corner of the state and it was felt that sufficient information was now available to pinpoint a number of areas of particular interest which could be examined on a major expedition. The Western Australian Museum in conjunction with the Field Museum of Natural History, Chicago, USA, conducted an intensive survey of the land, freshwater and marine fauna of the Admiralty Gulf and adjacent Mitchell Plateau from 16 October to 6 November 1976. The teams had a variety of interests: mammals, birds and reptiles, fish, insects, mites, and molluscs. This paper is the first report on the work done on molluscs during the expedition.

THE STUDY AREA

The Admiralty Gulf (Figure 1) is a large marine embayment with an area of approximately 1700 km^2 on the extreme northeast coast of Western Australia about 300 km W of the Northern Territory border. The waters of the Gulf are essentially marine but minor freshwater inflows are received from the Mitchell and Lawley Rivers; limited estuarine areas are associated with each river. The complex system of tides which occurs in the Gulf makes the area an interesting one for the examination of the patterns of zonation of marine intertidal mollusc species. The tidal range is extensive, with a maximum range of as much as 8.8 m on spring tides, from −1.7 m on the shore to +7.1 m. The average tidal amplitude is 4.4 m. The tides are predominantly semidiurnal, but diurnal tides occur during the changeover between neap and spring tide periods. When the changeover occurs the tidal levels remain static for several hours at a level of about +2.6 m.

Two major intertidal habitats occur in the Admiralty Gulf. A myriad of small bays is found, each with extensive mangrove development at the midtide levels. In many of the bays well developed mudflats occur landward of the

Figure 1

Map of Australia Showing the Position of the Admiralty Gulf. The Insert shows the Admiralty Gulf itself and the Location of Walsh Point in the Gulf.

L, Lawley River; M, Mitchell River; MI, Malcolm Island W, Walsh Point

mangroves. These areas are baked dry by the tropical sun during the neap tides but are submerged intermittently during spring tides. Few molluscs occur on or in the landward mudflats. Extensive mudflats which project seaward of the mangroves for as much as a kilometer are exposed by low spring tides. A variety of molluscs is found on the surface and in the mud of these flats. The headlands between the bays are rocky shores in the intertidal zones; the rock is of either sandstone or basalt, depending on the particular location in the Admiralty Gulf. Three marine programs were conducted in the Admiralty Gulf by the WAM Mollusc Department. The results of a faunal survey of the Gulf and the nearby Institut Islands and an intensive examination of the molluscs of the mangrove swamp at Port Warrender in the Gulf will be published elsewhere. The present paper examines the zonation of epifaunal marine gastropods at Walsh Point in the Admiralty Gulf.

Walsh Point is a small basaltic peninsula 2.7 km long (Figure 1) located at latitude 14°35′S and a longitude of 125°50′E. The seaward tip of Walsh Point, where the samples reported here were collected, is almost completely rocky in the intertidal areas. The shore of the high intertidal zone is composed of small rocks 5 to 13 cm in diameter which are several layers deep. These rocks are easily moved about by even moderate wave action. The rocks are larger at the midtide level, about 10 to 30 cm in diameter, and are only 2 or 3 deep. Base rock is exposed in some areas of the midtide zone. At the lower intertidal areas the basalt rocks are 30 cm or larger in diameter and are separated from each other by up to 30 cm of sand; very few rocks adjoin each other in the low intertidal zone. At a level of about 0.5 m the shore changes rapidly into a sandy beach in which rocks are rare.

Walsh Point is located well within the Admiralty Gulf and is thus protected from the wave action of the open sea. The water is extremely turbid at low tide even on calm days, with a visibility of 15 cm or less. As the tide rises, visibility increases to about 90 cm.

MATERIALS AND METHODS

Four transects approximately 10 m apart were made along the rocky shore of Walsh Point from the 0.5 m tide level to the 7.0 m level. The tide level was determined by comparison of the water levels at Walsh Point with tide charts for nearby Malcolm Island. A 1 m × 1 m quadrat was searched at every other meter along the transect and all gastropods found were removed and preserved in 10% formalin. All specimens were returned to the museum laboratories where they were identified and counted. Shell length of all individuals of *Nerita* was measured with vernier calipers. The resulting data were grouped into 0.5 m shore levels. Voucher specimens of all species collected have been deposited in the Western Australian Museum where they have catalogue numbrs WAM 1256-76 to 1274-76.

RESULTS

A total of 3375 individuals belonging to 18 species of gastropod molluscs was collected in the study. The density of each species and the standard deviation in each zone is given in Table 1. Three zones were demonstrated by the species: species which had their maximum level of abundance at the lowest tide level, then tapered off as the height on the shore increased; species with a maximum density near the midtide level whose densities decreased both above and below the midtide region; and species most abundant in the upper tidal levels whose density decreased below the hightide zone. The species comprising each zone will be discussed in turn.

Of the 18 species collected 10 had their maximum abundance in or near the lowest zone studied. Although a majority of species was restricted to this lowest tidal area, the numbers of individuals of each species were generally very low. The entire group was represented by 507 individuals, which was 15.0% of all gastropods collected. Included in this group is a number of minor species which were represented by 25 or fewer individuals: *Cantharus erythrostoma*, *Cantharidus strigatus*, *Columbella duclosiana*, *Haliotis varia*, *Onchidium daemelli*, *Pattelloida saccharina*, *Montfortula variegata*, and *Trochus lineatus*. The most abundant species in the low intertidal zone was *Morula margariticola*. This species had its maximum density in the lowest two zones (Figure 2), from 0.5 to 1.5 m on the shore, where it had an average density of 13.7/m². The density of *M. margariticola* decreased rapidly above this level, with only 3 individuals being found above the 2.5 m mark. The other abundant species in the lowest group, *Thais kieneri* (Figure 2), had a wider distribution which ranged from 0.5 to 4.5 m. This species was much less abundant than *M. margariticola* and had a maximum density of only 3.5/m² in the 1.5 to 2.0 m zone.

The second group of 6 species had their highest densities in the middle tidal ranges and were less abundant at both higher and lower levels on the shore. The midtide group was numerically dominant on the shore and accounted for 76.0% of all specimens collected. Four minor species are included in this group: *Monodonta labio*, *Morula granulata*, a species tentatively identified as *Cuma gradata*, and an unidentified thaiad species. The most interesting feature of the midtide group was the dominance of 2 species of the genus *Nerita*: *N. reticulata* and *N. undata*. *Nerita reticulata* (Figure 2) was the most abundant species collected in the study, being represented by 1300 individuals or 38.9% of all gastropods collected. *Nerita undata* (Figure 2) was second with 1090 individuals (32.3% of the total). Both species had a wide vertical range on the shore that encompassed virtually all of the zones studied. *Nerita reticulata* had low numbers of individuals below the 1.5 m mark and increased gradually in density to the 3.0 m level, after which the numbers dropped steadily. While it had essentially the same vertical range as *N. reticulata*, the zonation pattern of *N. undata* was very different (Figure 2). Low numbers of 4.8 and less per m² were encountered both below 2.5 m and above 5.5 m. Instead of a gradual increase toward the midtide level as was observed in *N. reticulata*, the number of individuals of *N. undata* was relatively constant at high levels of 16.0 to 20.3/m² between the 2.5 and 5.5 m levels. The maximum abundance of *N. reticulata* occurred in the 2.5 to 3.0 m level, one step below the highest density of *N. undata*. While the mean heights of the populations of the 2 species were different, *N. reticulata* had a mean of 3.0 ± 2.5 m and *N. undata* was 3.9 ± 2.6 m, the differences were not statistically significant (t-test, 0.05 level).

Only 2 species had their maximum abundances in the upper intertidal levels and together they constituted only

Table 1

Density (No./m²) of Marine Gastropods in the Intertidal Zone of Walsh Point, Admiralty Gulf, Western Australia, With one Standard Deviation from the Mean Indicated for all Zones in which more than Four Individuals of a Species were Found. The Level of Maximum Density of a Species is enclosed by a Square

Species	Height above datum (m)												
	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0	6.0-6.5	6.5-7.0
							Lower intertidal species						
Cantharidus strigatus	**0.3**	0.1	0.1	0.1	0.1								
Cantharus erythrostoma Linnaeus, 1758	**1.3 ±1.0**	0.6 ±1.3	0.1										
Columbella duclosiana		**0.3**											
Haliotis varia Linnaeus, 1758	**0.2**	0.1	0.1	0.1	0.1								
Montfortula variegata Adams, 1852	0.1	0.1	0.2	**0.4**	0.3								
Morula margariticola Broderip, 1832	**14.6 ±5.5**	12.9 ±8.5	3.4 ±3.5	2.4 ±1.1	0.3	0.1							
Onchidium daemelli Semper, 1882	0.2	0.3	**0.6**	0.5									
Patelloida saccharina (Linnaeus, 1758)		0.1	0.1	0.1	0.1								
Thais kieneri Deshayes, 1844	0.9 ±1.2	1.7 ±1.6	**3.5 ±2.3**	1.5 ±1.1	1.4 ±1.3	1.4 ±0.7	0.1	0.3					
Trochus lineatus Lamarck, 1822			**0.1**										
							Middle intertidal species						
cf. *Cuma gradata*	0.3	0.1	0.5 ±0.6	0.8 ±0.4	0.8 ±1.1	0.4	**2.3 ±2.3**	1.0 ±2.7					
Monodonta labio Linnaeus, 1758	0.1		0.3	0.4	1.8 ±1.5	**3.0 ±1.4**	2.5 ±1.7	0.8 ±1.4	0.3				
Morula granulata Duclos, 1832								**0.1**					
Nerita reticulata Karsten, 1789	5.0 ±14.4	7.6 ±9.4	12.8 ±14.3	13.4 ±9.6	**35.9 ±10.2**	32.5 ±14.3	20.8 ±13.2	11.7 ±9.0	3.8 ±5.0	0.4 ±0.4	0.3		
Nerita undata Linnaeus, 1758		0.5 ±0.6	1.3 ±1.8	4.8 ±5.0	17.9 ±7.3	**20.3 ±9.7**	19.5 ±6.1	19.3 ±6.0	17.6 ±9.2	16.3 ±8.9	3.4 ±3.0	1.5 ±1.9	
Thaiad Species 1		0.3	0.6 ±0.6	0.4 ±0.5	**2.4 ±2.6**	1.0 ±1.0	1.0 ±0.9	0.3					
							Upper intertidal species						
Nerita polita Linnaeus, 1758							0.3	1.1 ±0.5	0.6 ±0.4	**2.3 ±1.9**	1.5 ±2.2	0.6 ±0.5	
Planaxis sulcatus (Born, 1780)	0.3						1.1 ±2.6	3.5 ±3.6	3.3 ±5.4	**10.5 ±6.4**	5.8 ±8.4	1.4 ±3.0	
Total density	23.3 ±11.7	24.7 ±10.8	23.7 ±17.5	24.9 ±10.1	**61.1 ±11.3**	58.7 ±25.8	47.6 ±1.8	38.1 ±18.4	25.6 ±18.4	29.5 ±18.5	11.0 ±10.9	3.5 ±3.8	

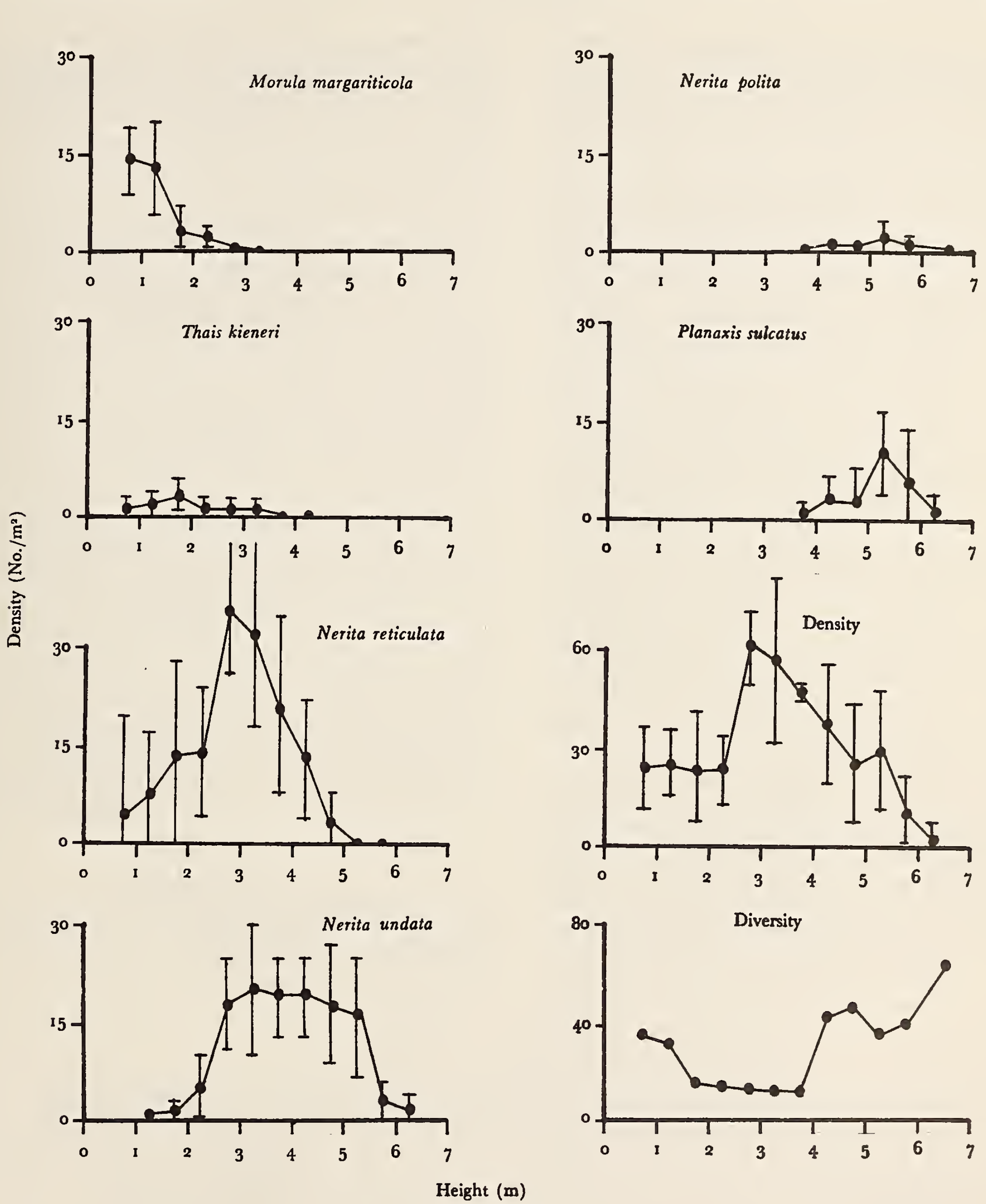

Figure 2

Zonation of Marine Gastropod Species at Walsh Point, Admiralty Gulf, Western Australia, Showing the Density of Each Species at the Various Tidal Heights. Densities Shown are Means and the Standard Deviation for Each Mean is Indicated

9.0% of all gastropods collected. Both *Nerita polita* (Figure 2) and *Planaxis sulcatus* (Figure 2) were found from 3.5 to 6.5m on the shore and had their maximum concentrations in the zone of 5.0 to 5.5m. *Planaxis sulcatus* was the dominant member of this group, being 4 times as abundant as *N. polita.*

The total density of gastropods (Figure 2) was moderate in the lower intertidal levels, ranging from $24.3/m^2$ at the 0.5 to 1.0m level to $24.9/m^2$ at the 2.0 to 2.5m interval. Density in the next shore zone more than doubled to $61.1/m^2$, largely due to increases in the densities of *Nerita undata* and *N. reticulata*. The fact that the total abundance of gastropods declined steadily above the 3.0m mark is a further indication of the numerical dominance of these 2 midtide species. A Simpson's (1949) index of diversity was calculated for each of the intertidal zones. Maximum diversity, where each individual belongs to a different species, is indicated by a value of 0 on the Simpson index; minimum diversity, where all individuals are of the same species, has a value of 1. The diversity index closely paralleled the total gastropod density (Figure 2). The midtide region of highest density was also the area of highest diversity. Diversity was lower both above and below the midtide region, as was the total density. The index is designed to prevent the total number of individuals studied from influencing the index of diversity. Thus the higher diversity in the midtide region is real and is not simply an artifact of the higher number of individuals which occurred there.

One of the most interesting features that can be examined with a study of this type is the partitioning of the environment by groups of closely related species in a sympatric association with each other. Two such groups were identified in this investigation. Four species of thaiad: *Cuma gradata* (tentative identification), *Morula granulata*, *M. margariticola*, and an unidentified species, occurred in the middle and lower intertidal regions. Despite the fact that they are all carnivorous species in the same subfamily, the thaiads belong to 3 different genera and are not closely related taxonomically. Together they comprised only 16.1% of all gastropods collected. More interesting are the 3 species of the herbivorous genus *Nerita* which feed by rasping algal material off the surfaces of the rocks on which they live. In contrast to the thaiads the nerites all belong to the same genus and numerically dominated the study, accounting for 72.9% of all gastropods collected.

A number of studies (*e. g.* Edwards, 1969) of intertidal gastropods have demonstrated that smaller individuals of a species tend to be concentrated on the lower shore areas and larger specimens tend to be located higher in the intertidal zone. Lower intertidal areas are covered by seawater for a greater length of time during each tidal cycle than the areas higher up, providing a more gentle environment for a marine species. Juvenile individuals are generally more susceptible to variations in condi-

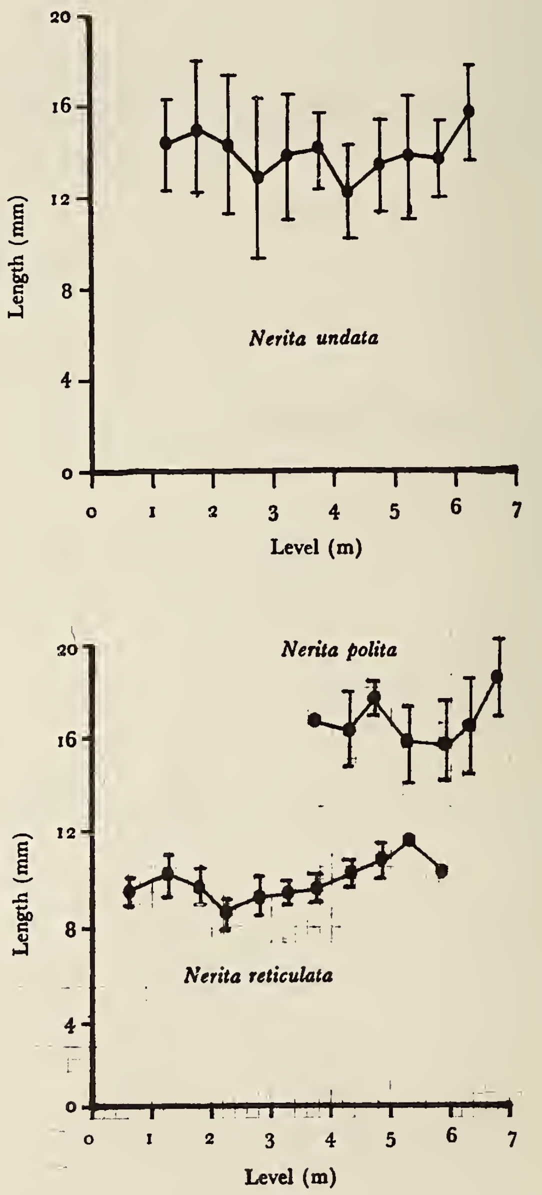

Figure 3

Mean Lengths of the Three *Nerita* Species Collected at Walsh Point, Admiralty Gulf, Western Australia. For Each Tidal height a Standard Deviation of the Mean is Indicated for Every Sample of More than Five Individuals tions than are the adults, which usually have greater environmental tolerances. Thus the mean sizes of each of the 3 *Nerita* species would be expected to increase as the area sampled moved up the shoreline, but this was not the case (Figure 3). The mean sizes of each species were stable throughout the tide levels and no demonstrable trends were evident, indicating that juveniles were not in fact found lower on the shore than adults, but there was a distinct tendency for very large individuals of each species to be concentrated in the upper meter of the species' range. The species themselves demonstrated a clear increase in size with tidal height (Table 2). The average length of all *N. reticulata* measured was 9.4±0.7mm. This species was the lowest on the shore with a mean tidal height of 3.0±2.5m. The intermediate *N. undata* at 3.9 ±2.6m averaged 13.0±2.1mm, 1.4 times as large as *N. reticulata*. *Nerita polita*, which was highest on the shore at 5.2±0.2m, averaged 16.1±1.6mm, 1.2 times as large as *N. undata*.

The index of diversity devised by Simpson (1949) was modified by Morisita (1959) as the basis of an index of overlap; the appropriateness of the overlap index has been discussed by Horn (1966). The overlap index developed by Morisita (*op. cit.*) has been used to determine the degrees of overlap between the populations of the 3 *Nerita* species on the shore of Walsh Point (Table 2). The 2 species which occur at opposite ends of the shore, *N. reticulata* and *N. polita*, had the lowest overlap, 0.07. *Nerita undata* occupied an intermediate position on the shore and had a high overlap with both *N. reticulata* below and *N. polita* above.

DISCUSSION

The diversity of gastropods was highest in the midtide areas and tapered off towards both the higher and lower portions of the shore. One would expect diversity to be highest in the lowest intertidal areas which are covered by seawater for the longest periods during each tidal cycle. Reimer (1976), for example, studied the intertidal fauna on rocky shores on the Pacific coast of Panama. Of 220 species identified, 42% were found exclusively in the lower intertidal zone, 17% were limited to the midlittoral and only 6% were exclusive to the upper shore. The remaining species had distributions that overlapped at least 2 zones. The lower intertidal zone had the highest diversity and the splash zone the lowest. The unexpectedly low diversity in the lower intertidal zone of the Admiralty Gulf can be easily explained in terms of the beach structure. The rocks of the midtide region are large enough that they are not rolled about by waves except during storms. With one rock lying on another there is an abundance of crevices and nooks and crannies for the snails to retreat into during the emersion at low tide. In the lower portion of the intertidal zone the rocks are spaced about 30cm apart, eliminating the availability of refuges in the gaps between adjacent rocks. The index of diversity is based on the quantitative samples in which only 18 of the most common gastropod species were found. Intense collection in the area for the report on the molluscan fauna of the Admiralty Gulf has shown that at least 75 gastropod species occur at Walsh Point.

The dominance of the 3 *Nerita* species was overwhelming: *N. reticulata* constituted 38.9% of all gastropods collected and *N. undata* 32.3%. *Nerita polita* was a minor species at 1.8%. The dominance of the 3 congeneric species raises the question of how they partition the available resources and which factors are potentially limiting. The population of *N. polita* is partially segregated spatially from the other 2 species. *Nerita polita* is an upper intertidal species with a mean population level of 5.2±0.2m, above the levels of *N. reticulata* and *N. undata*.

Table 2

Characteristics of the Populations of *Nerita* at Walsh Point, Admiralty Gulf, Western Australia

	Shell length			Shore height			Niche overlap	
	Minimum (mm)	Maximum (mm)	Mean ± 1 SD (mm)	Minimum (m)	Maximum (m)	Mean ± 1 SD	Index	Species
Nerita reticulata	4	12	9.4±0.7	0.5	6.0	3.0±2.5	0.07	*Nerita reticulata*—*Nerita polita*
Nerita undata	3	22	13.0±2.1	1.0	6.5	3.9±2.6	0.29	*Nerita undata*—*Nerita polita*
Nerita polita	11	22	16.1±1.6	3.5	7.0	5.2±0.2	0.35	*Nerita reticulata*—*Nerita undata*

The index of overlap between *Nerita polita* and *N. reticulata* was very low, only 0.07. The overlap between *N. polita* and *N. undata*, which occupies the intermediate position on the shore is much higher, 0.29, indicating a considerable overlap. Populations of the 2 dominant nerites, *N. reticulata* and *N. undata*, are also somewhat segregated vertically, with *N. undata* being higher on the shore (3.9 ±2.6m) than *N. reticulata* (3.0±2.5m), but the overlap between populations was substantial. Both occurred at virtually every tide level sampled. The maximum density of *N. undata* was in the 3.0 to 3.5m tide level, one zone above the maximum abundance of *N. reticulata*. The index of niche overlap was high, 0.35, reflecting the substantial mixing of the populations.

Most studies of density regulation of intertidal gastropods have been done on limpets. Frank (1965) showed that the density of the limpet *Acmaea digitalis* Rathke, 1833, was limited by an interaction of space and food resources. This appears to be a general condition in limpets. Underwood (1975; 1976) found density regulation in *Nerita atramentosa* Reeve, 1855, to be a function of food competition. Significant natural mortality was only found in the adults of the population. Underwood suggested that if the density of *N. atramentosa* was increased above the critical level by excessive numbers of juveniles settling on the shore the growth rates of the juveniles would be slowed and adult mortality would increase until the population had returned to normal levels. *Nerita atramentosa* feeds on diatoms and algal spores which are thought to be replenished on each high tide (Underwood, 1975; 1976). The exact food of the 3 *Nerita* species of the Admiralty Gulf is unknown, but their radular structure is similar to that of *N. atramentosa* and it is reasonable to suggest that food could also be a limiting factor for the Admiralty Gulf species. Food competition would be lessened by the differences in mean tidal height of the 3 species, which means that each is concentrating its feeding on a different shore level. Another possible factor in reducing competition is differences in the behavior of the species. This possibility has not been examined in the present study. Coleman (1976) reported on the activity patterns of 3 species of *Nerita*: *N. albicilla* Linnaeus, 1758; *N. plicata* Linnaeus, 1758, and *N. polita*. All 3 actively move about while immersed at high tide and during the initial stages of emersion as the tide falls. When the rocks dry during low tide, the snails retreat into sheltered areas and become quiescent. While the pattern of behavior of the 3 species is similar, the selection of sheltered areas varies between species: *N. plicata* congregates in crevices and hollows; *N. albicilla* remains in damp, shaded crevices; and *N. polita* tends to burrow into the sand. If similar behavioral differences are operating in the species found in the Admiralty Gulf they could influence the areas grazed by each species.

A number of nerite species occurs along the rocky shores of the Western Australian coastline (Wilson & Gillett, 1974). *Nerita atramentosa* is a cold water species which is widely distributed along the south coast and extends northward along the west coast as far as Point Cloates. *Nerita albicilla, N. plicata, N. polita, N. reticulata,* and *N. undata* are all tropical species which have a range extending across the entire tropical north coast of the state and range southwards on the west coast. The numerous possible interactions between these 6 species offer a wide range of interesting avenues of investigation. Possible behavioral differences and mechanisms of density regulation have already been mentioned. Varying combinations of the nerites occur at various localities along the northwestern coasts of the state. It would be interesting to investigate the populations of several species for evidence of character displacement. Fenchel (1975) has shown that character displacement occurs in the gastropod genus *Hydrobia* where mean individual sizes of the species change when 2 or more species are present. A similar factor could be operating in *Nerita*: *N. undata* averaged 1.4 times the mean shell length of *N. reticulata*, and the average *N. polita* was 1.2 times as large as *N. undata*. The sizes of all 3 species in the Admiralty Gulf were well below the maximum sizes reported by both Cernohorsky (1972) and Wilson & Gillett (1974). A second possible mechanism of character displacement is a change in the mean shore level of a nerite species when it occurs with one or more other nerites. Particularly interesting in this regard is *N. atramentosa* which is the only nerite on most shores, where the population is centered in the low intertidal zone (Prideaux, 1976). It would be interesting to see if the population of *N. atramentosa* is forced to lower shore levels by competitive interaction with other nerites in areas where it is sympatric with other species of *Nerita*.

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Literature Cited

Cernohorsky, Walter Oliver
1972. Marine shells of the Pacific, vol. 2, 411 pp.; 68 plts. Pacif. Publ. Sydney, Austral.

Coleman, Noel
1976. Aerial respiration of nerites from the north-east coast of Australia. Austral. Journ. Mar. Freshwater Res. 27: 455 - 466

Edwards, Dallas Craig
1969. Zonation by size as an adaptation for intertidal life in *Olivella biplicata*. Amer. Zool. 9: 399 - 417

Endean, Robert W., W. Stephenson & R. Kenny
1956. The ecology and distribution of intertidal organisms on certain islands off the Queensland coast. Austral. Journ. Mar. Freshwater Res. 7: 317 - 342

Fenchel, Tom
1975. Character displacement and coexistence in mud snails (Hydrobiidae). Oecologia (Berlin) 20: 19 - 32

Frank, Peter Wolfgang
1969. Growth rates of some gastropod molluscs on the coral reef at Heron Island. Oecologia (Berlin) 2: 232 - 250

Hodgkin, Ernest P., Loisette M. Marsh & G. G. Smith
1955. Rottnest Island: .The Rottnest Biological Station and recent scientific research. 19. The littoral environment of Rottnest Island. Journ. Roy. Soc. West. Austral. 42: 85 - 88

Horn, Henry S.
1966. Measurement of "overlap" in comparative ecological studies. Amer. Nat. 100: 419 - 424

Marsh, Loisette M. & Ernest P. Hodgkin
1962. A survey of the fauna and flora of rocky shores of Carnac Island, Western Australia. West. Austral. Nat. 8: 62 - 72

Morisita, M.
1959. Measuring of interspecific association and similarity between communities. Mem. fac. Sci., Kyushu Univ. Ser. E (Biol.) 3: 65-80

Prideaux, Peter
1976. The role of competition in the structure of communities of prosobranch gastropods at Strickland Bay, Rottnest Island. B. Sci. Thesis, Univ. West. Austral., 47 pp.

Reimer, A. A.
1976. Description of a *Tetraclita stalactifera panamensis* community on a rocky intertidal Pacific shore of Panama. Mar. Biol. 35 (3): 225 - 238

Simpson, E. H.
1949. Measurement of diversity. Nature, London 163: 688

Stephenson, T. A. & Anne Stephenson
1949. The universal features of zonation between tide-marks on rocky coasts. Journ. Ecol. 37: 289 - 305

Underwood, Anthony J.
1972. Tide-model analysis of the zonation of intertidal prosobranchs. II. Four species of trochids (Gastropoda; Prosobranchia). Journ. exp. mar. Biol. Ecol. 9: 257 - 277
1975. Comparative studies on the biology of *Nerita atramentosa* Reeve, *Bembicium nanum* (Lamarck) and *Cellana tramoserica* (Sowerby) (Gastropoda; Prosobranchia) in S. E. Australia. Journ. exp. mar. Biol. Ecol. 18: 153 - 172
1976. Food competition between age-classes in the intertidal neritacean *Nerita atramentosa* Reeve (Gastropoda; Prosobranchia). Journ. exp. mar. Biol. Ecol. 23: 145 - 154

Wilson, Barry R. & Keith Gillett
1974. Australian Shells. 168 pp.; illus. Sydney, Australia (A. H. & A. W. Reed)